THE ORIGIN OF THE PTERIDOPHYTE FLORA OF CENTRAL AMERICA

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The biogeographical relationships among the Central American pteridophytes were first suggsted by Hermann Christ in his introduction to the ferns and fern-allies in *Primitiae Florae Costaricensis* (Bommer & Christ, 1896). Christ distinctly identified among his collections those elements considered by him to be of Mexican origin and those he thought best represented the South American vegetation.

In his Geographie der Farne, Christ (1910) published his interpretation of the Central American fern flora, mostly based on the ideas of Carl Werckle (1909), with whom Christ corresponded, and who identified a Mesoamerican vegetational type as quite different from both the true Mexican and the South American counterparts. Winkler (1938) augmented Christ's dicta with the addition of many new records.

Recently, Tryon (1972) published on the geographical distribution of the continental pteridophytes and defined Central America as one of his regional centers (Fig. 1), based on the evaluation of some 400 taxonomic units extracted from floras, monographs and herbaria. In 1975, Lellinger proposed a phytogeographical analysis of the Chocó vascular cryptogam flora, which resembles that of the Costa Rican and Panamanian floras. Both Tryon and Lellinger rely heavily on the comparison of lists of species, a method which, in my opinion, can only partly reflect the vegetational history of an area.

Rather than repeating their comparative researches and thus reaching similar results, I intend to outline the processes by which Central America has become one of the richest and most complex floristic areas of the world. I begin with the following two premises: a) the Pteridophyta is a very ancient group of plants that probably originated in tropical environments; b) because of geological events, Central America can be divided into an older, northern portion known as Nuclear Central America (Vinson & Brineman, 1963) and a southern, younger territory that comprises the southern parts of Nicaragua, all of Costa Rica, and much of Panama. I believe the first statement will require no further explanation, and the second has had an excellent exposition by Dr. Coney (this symposium, also see Weyl, 1980). Tryon (1972) presented sufficient evidence of the strong affinities between the current Mexican, Central American, and South American floras. I only would like to challenge some of his interpretations, particularly those concerning his definition of "centers for speciation" and his conclusions regarding long range dispersal in such generalized terms.

CONTINENTAL DRIFT

The land masses of North and South America acquired their stock of pteridophytes during the Carboniferous, when the continents shared a common flora.

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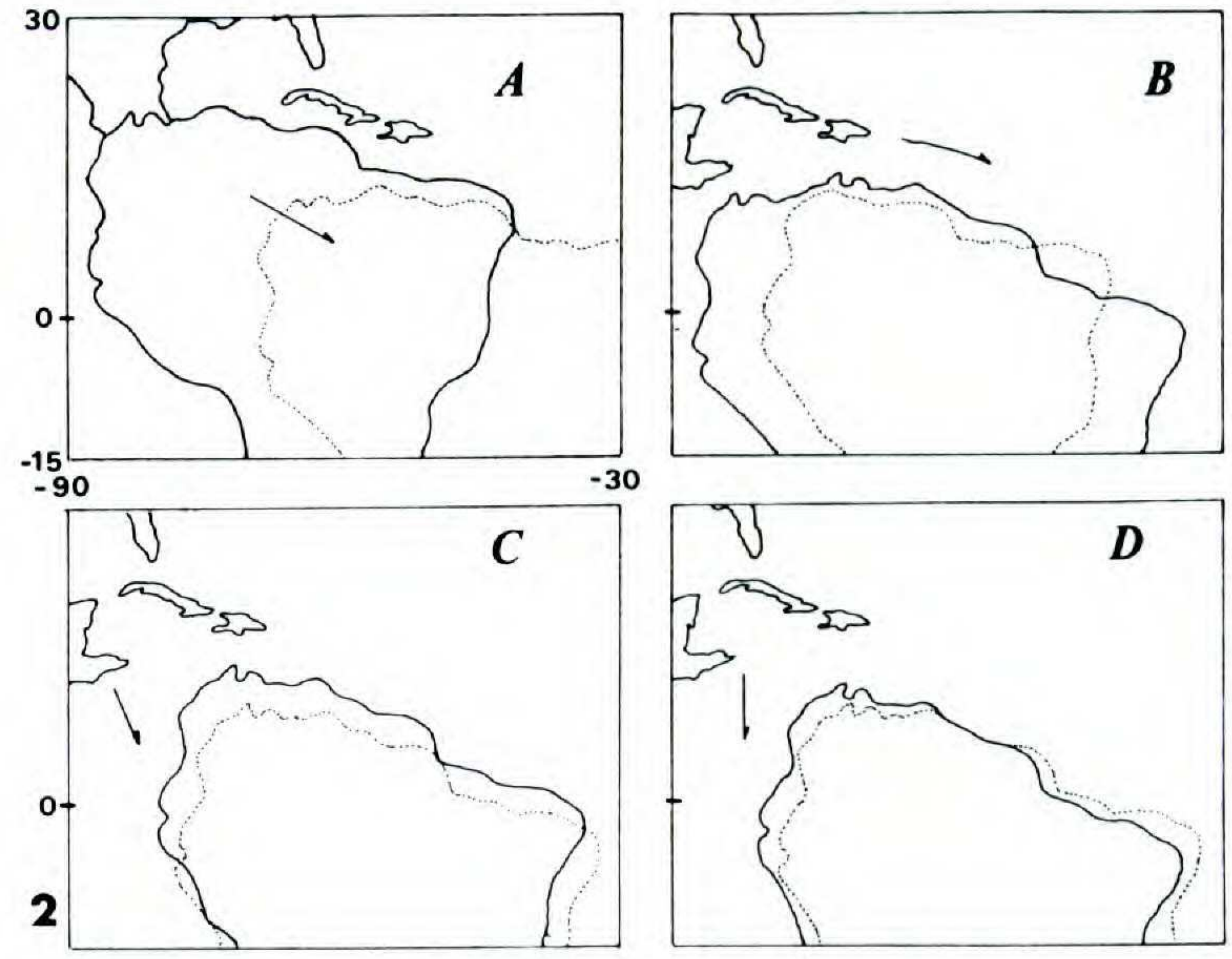

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FIGURES 1–2.—1. Tryon's (1972) regional centers of continental tropical American ferns: 1—Mexican, 2—Central America, 3—Andean, 4—Guyanan, 5—Brazilian. All except 2, 4 considered as primary centers.—2. Relative motion of South America from Early Jurassic to Late Tertiary. a) Hettangian-Valanginian (180–127 m.y. B.P.), b) Valanginian-Coniacean (127–84 m.y. B.P.), c) Santonian-Eocene (84–38 m.y. B.P.), d) Oligocene-Miocene (38–0 m.y. B.P.).

Fossil records attest to intercontinental plant migrations under more or less homogeneously tropical and subtropical climates (e.g., fossilized remains of palms, cycads, and tropical ferns in areas now in the Arctic and Antarctic). At the turn of the Upper Carboniferous, the continents had drifted well apart and those ancient groups began their speciation and adaptation through isolation, giving place to disjunctions and extinctions as well as to some pantropical distributions. For example, Cyatheaceae are well distributed; Loxsomaceae are disjuncts between New Zealand, Bolivia, and Costa Rica; Matoniaceae are at present found only in the Old World tropics but were once common in Mexico and Colombia (Tomasini, 1981; van der Hammen, 1961a).

In the New World, continental drift not only separated Central America from the palaeotropics but also caused a north to south movement of the north and south cratons (Fig. 2), each portion carrying an ancestral stock of the same flora. Some of the present day interpretations of long range dispersal may be just the results of such partitioning and migration of the continental land masses, for instance, in the heterosporic fern-allies such as the *Selaginella rupestris* group, *Isoëtes mexicana-gardneriana* group, some lycopods, and some ferns.

During this time of southward migration, emergent lands were subjected to a succession of relatively rapid environmental changes related to latitudinal displacement (Fig. 3) resulting in speciation through adaptation and in expansion of the flora depending on their proximity to larger land masses. In Honduras, the fossiliferous beds show a remarkable array of plant groups that denounce climatic variability and floristic influences, particularly in the San Juancillo coal layers.

By various processes, the northern geosyncline filled up with materials from the North American craton bringing the southern limit of Nuclear Central America much further south than usually thought, the only aspect in which I do not agree with Dr. Coney, as I place that limit somewhere in the middle of Nicaragua

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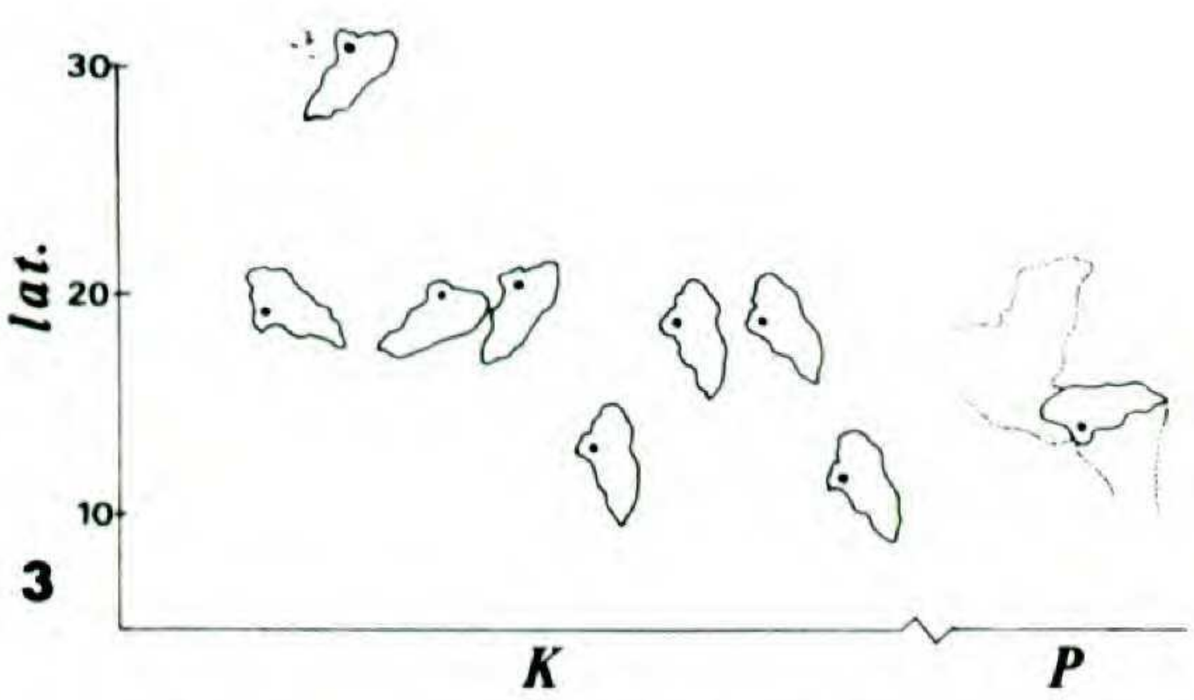

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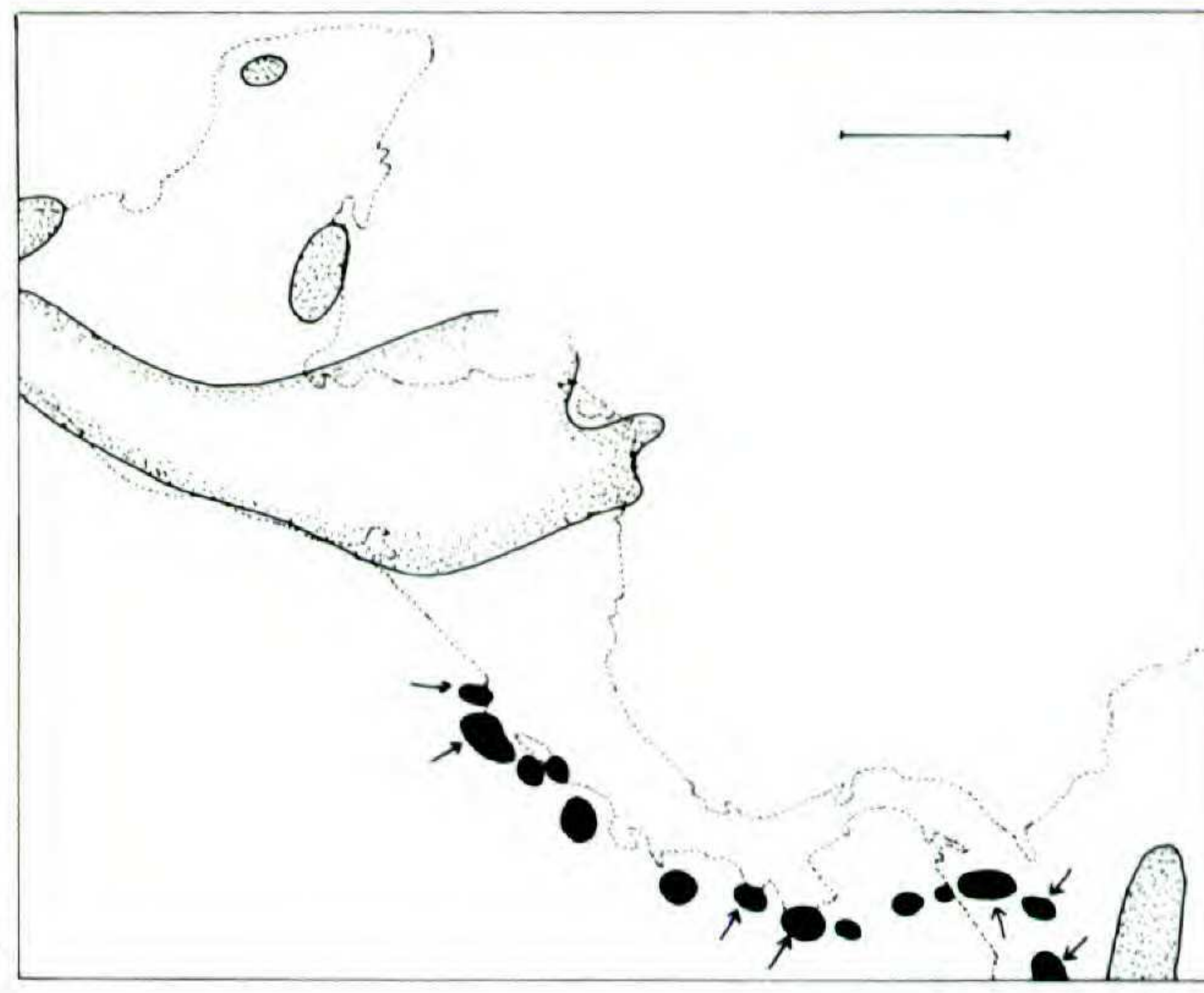

FIGURES 3–4.—3. The position of Honduras during part of the Cretaceous (K) relative to its present position (P). The dot marks a geographical point.—4. Palaeogeography of the Upper Cretaceous. Lines indicate the emerged lands. Solid areas represent volcanic islands, the arrows point to those still extant.

just north of the Lake Nicaragua, more or less coinciding with the natural austral limit of the genus *Pinus*. Likewise, the Andean geosyncline augmented the already rising volcanic edifices in the area now occupied by Colombia. In the Middle to Upper Cretaceous, the gap between the North and South American continents was beginning to diminish (Fig. 4).

CENTRAL AMERICA, ISTHMUS AND LAND BRIDGE

By the Miocene, both the north and south continents had reached their present positions and had had enough time, if time be needed, for their floras to speciate

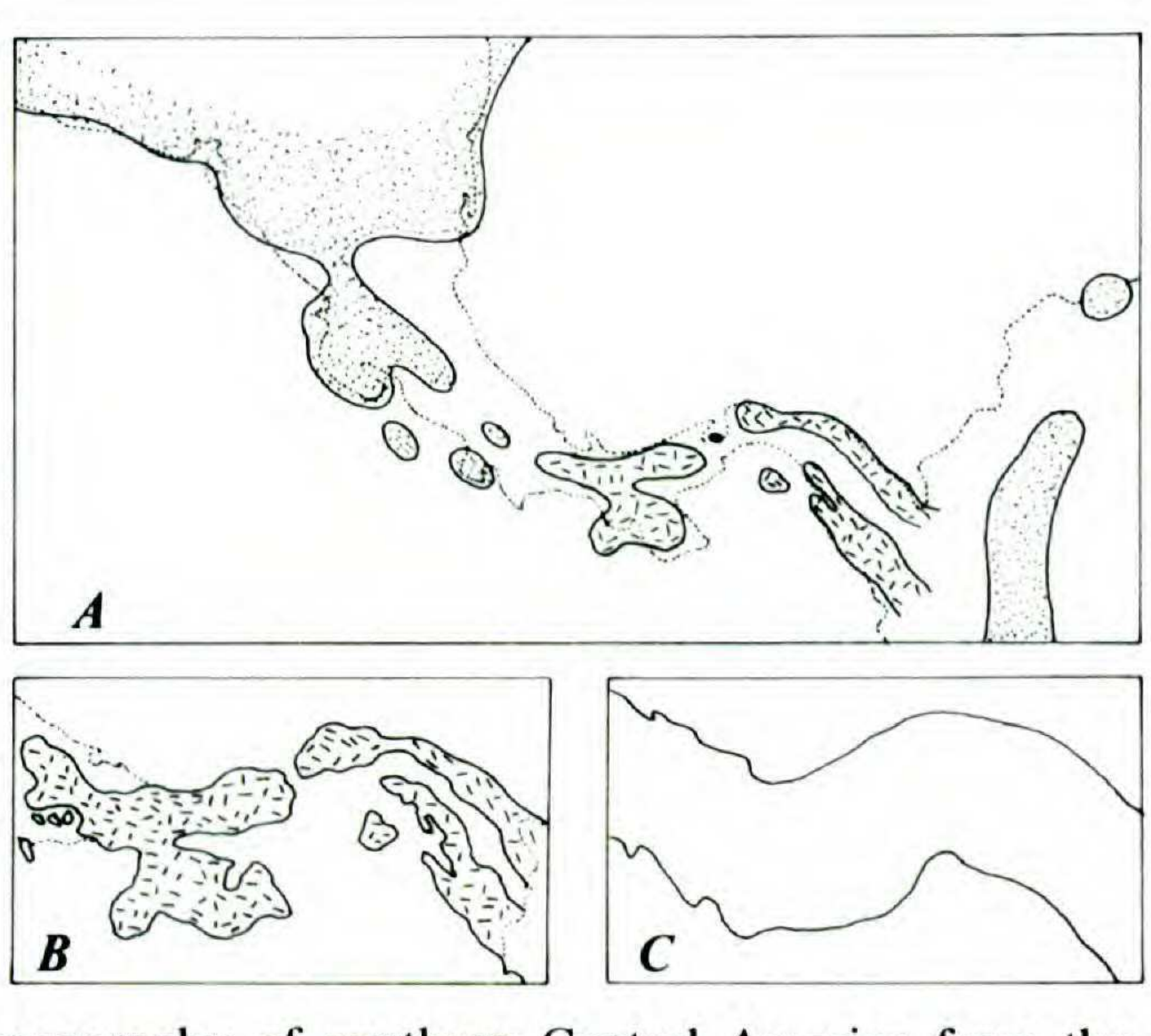

FIGURE 5. Palaeogeography of southern Central America from the Upper Oligocene to the Lower Miocene. Dotted areas indicate emergent lands. Broken lines indicate deposits of volcanic rocks, submarine or emergent.—B. Panama during the Upper Oligocene, emergent areas consisted of volcanic sediments.—C. Panama during the last marine regression of the Quaternary. The land bridge is by then completed and without gaps.

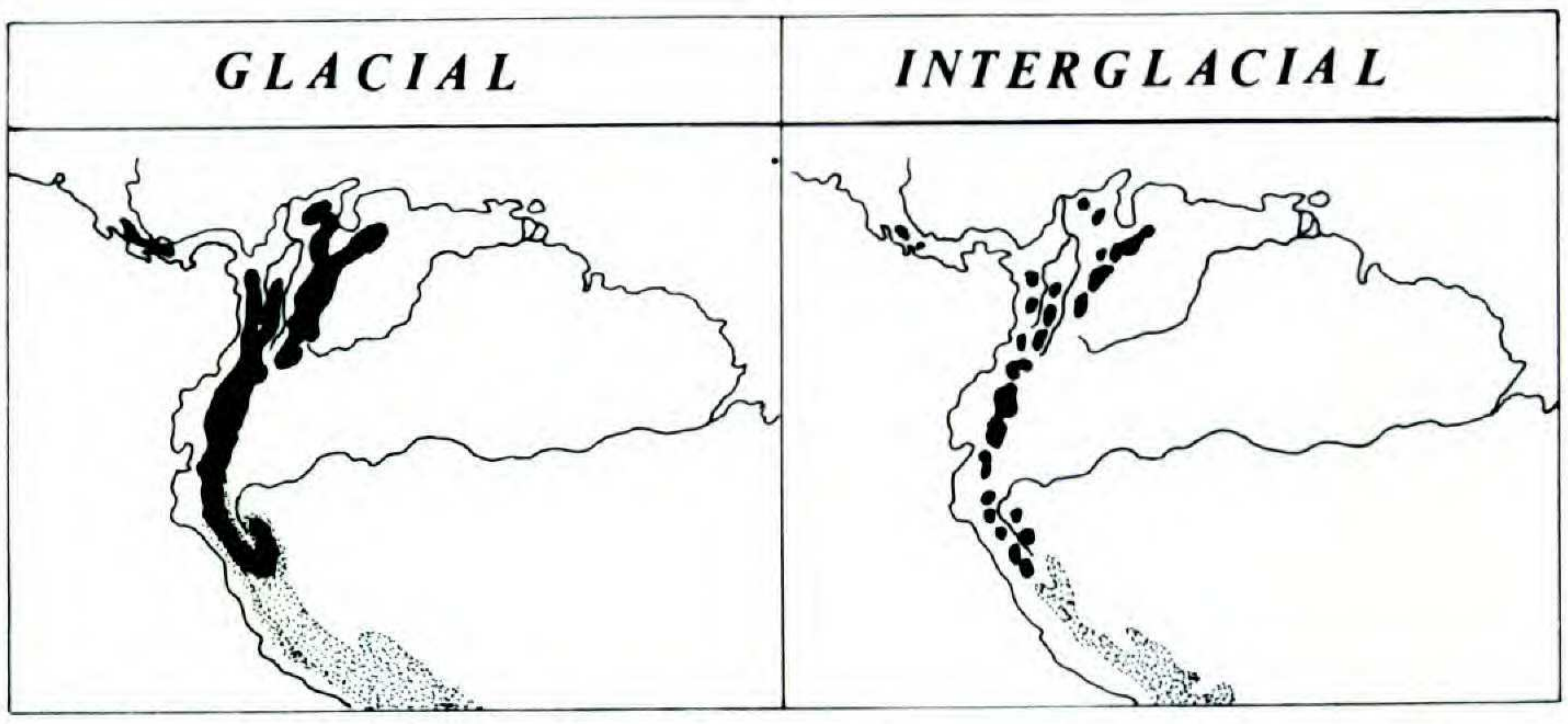

FIGURE 6. Distribution of paramos and punas during and after the last glaciation. Solid areas represent paramo, dotted areas are the punas (taken from Vuilleumier, 1981, modified).

and evolve enough to become distinctively the North American-Mexican elements, the Greater Caribbean element, and the South American element, the latter subdivided both geographically and climatically into Amazonian, Andean, and Patagonian. Those parts of North and South America that remained within the Tropics developed a rich pteridophyte flora both by geographic isolation and peripheral speciation.

The geosynclinal phenomena, coupled with intense volcanic activity and the interactions of the Cocos and Caribbean Plates, started the outcropping of the Central American isthmus south of middle Nicaragua and north of Colombia in a fast succession of events (Fig. 5), which produced the final land bridge between North and South America. This bridge was the stage of one of the greatest migratory phenomena of all ages, permitting the north-south-north passage of flora and fauna well known to us all (Simpson, 1980).

It is at this stage that it is necessary to look, albeit briefly, into the Caribbean-Central America relationship, which corresponds to two different geological causes, that of Continental Drift and plate tectonics for the Greater Antilles, and Late Tertiary volcanic phenomena for the Lesser Antilles. The floristic links between those Caribbean islands and Central America has been studied and documented for the Angiosperms elsewhere (Howard, 1973), and partially for the ferns by Tryon (1972). Few pteridophytes, other than cosmopolitan species, are shared by Antilles and Central America, *Adenoderris, Fadyenia, Neurodium,* some species of *Anemia* and *Lygodium,* the *Selaginella pallescens-harrisii* complex, species of *Botrychium* (e.g., *B. jenmanii, B. alabamensis* complex), *Lycopodium serratum,* etc., all serve as examples of Mexican-Caribbean-Central American exchanges. The rise of the Lesser Antilles by a series of volcanic events resulted in a bridge from northeast South America to Yucatan via the Greater Antilles, thus influencing circumcaribbean migrations under mediterranean conditions (Kruckow, 1980).

CLIMATIC INFLUENCES

The drastic climatic changes that took place during the Pleistocene greatly influenced massive migrations through the already completed and available Central American land bridge (van der Hammen, 1961b). There is no reason to ex-

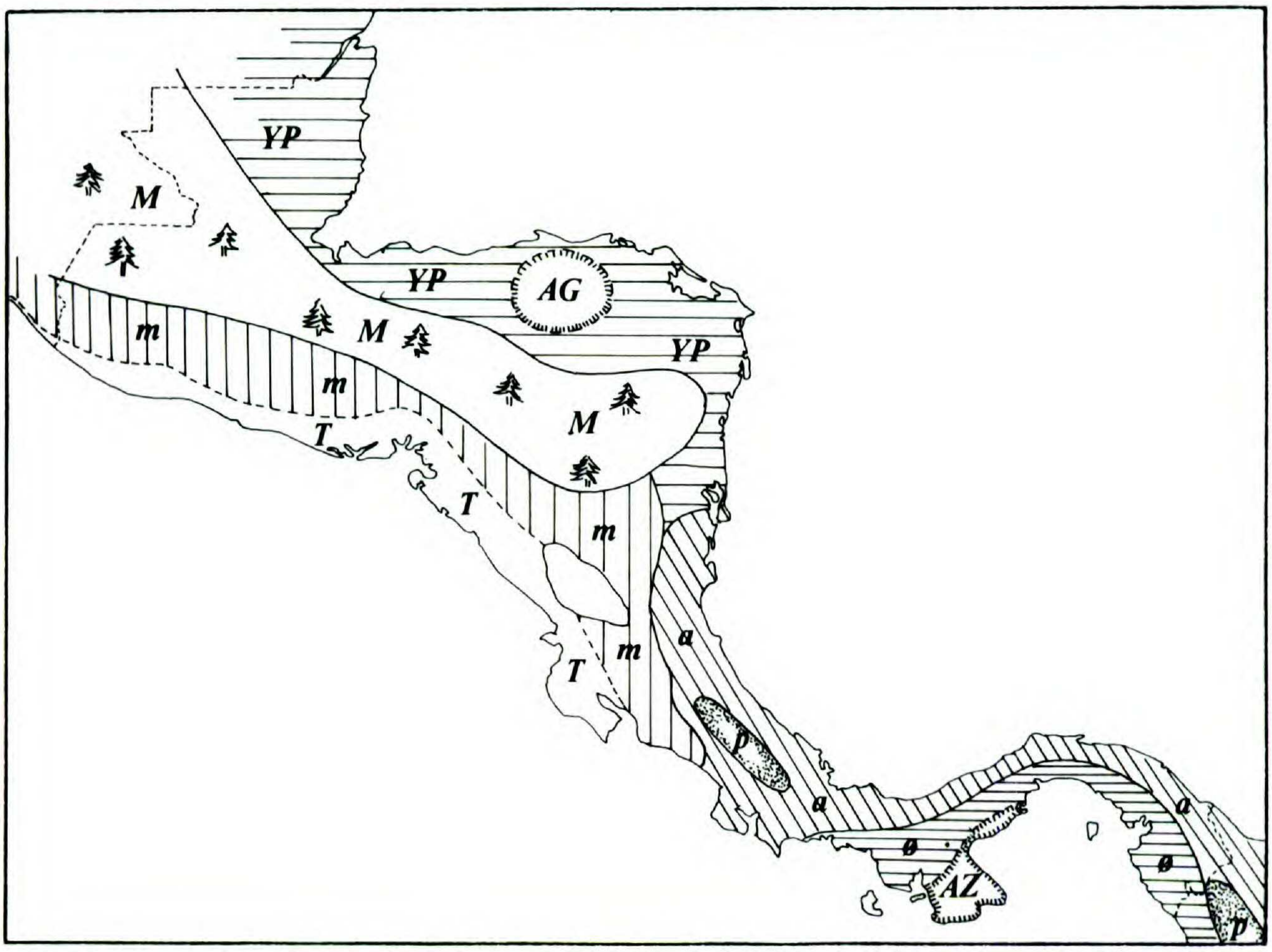

FIGURE 7. Vegetational types of Central America. T—The Tehuantepec xeric-sub arid vegetation; M—Mexican central highland elements, delimited by natural distribution of *Pinus*; m—Mexican mid-elevation elements; YP—the Yucatan/Peten flora; a—amazonian; ø—mixed Pacific South America and Amazonian; p—South American paramos or Andean elements. AG—the dry Pacific related flora of the Aguan valley in Honduras. AZ—Azuero in Panama is more closely related to the Venezuelan Llanos and northern South American savannas of the eastern coast.

clude vegetation from such migratory movements toward more favorable climates, if the latter are understood as more or less homogeneous higher temperatures and evenly distributed higher rainfall, such a favorable climate was prevalent in the Isthmus, which was and still is climatically moderated by two ocean fronts.

Glaciation proved important inasmuch as it affected the higher mountain ranges, creating the environmental conditions propitious to the migration and establishment of Andean elements, as well as some temperate, northern migrants, in what is a classical example of the compensatory effect of altitudes instead of higher latitudes. For example, the core analyses of Martin (1960) indicated that paramo-type vegetation existed in Costa Rica more or less 600 m below its present limits. This undated finding was further corroborated by Vuilleumier (1981; Fig. 6), whose findings apply also to ferns, such as: *Lycopodium saururus*, *L. brevifolium*, *Jamesonia* spp., and *Eriosorus* spp., found mixed with northern pteridophyta, e.g., *Hypolepis*, *Polystichum*, and *Odontosoria*, all Mexican elements, and even with some nearctic ones (*Asplenium monanthes*, *Cystopteris fragilis*, *Pellaea* spp., etc.).

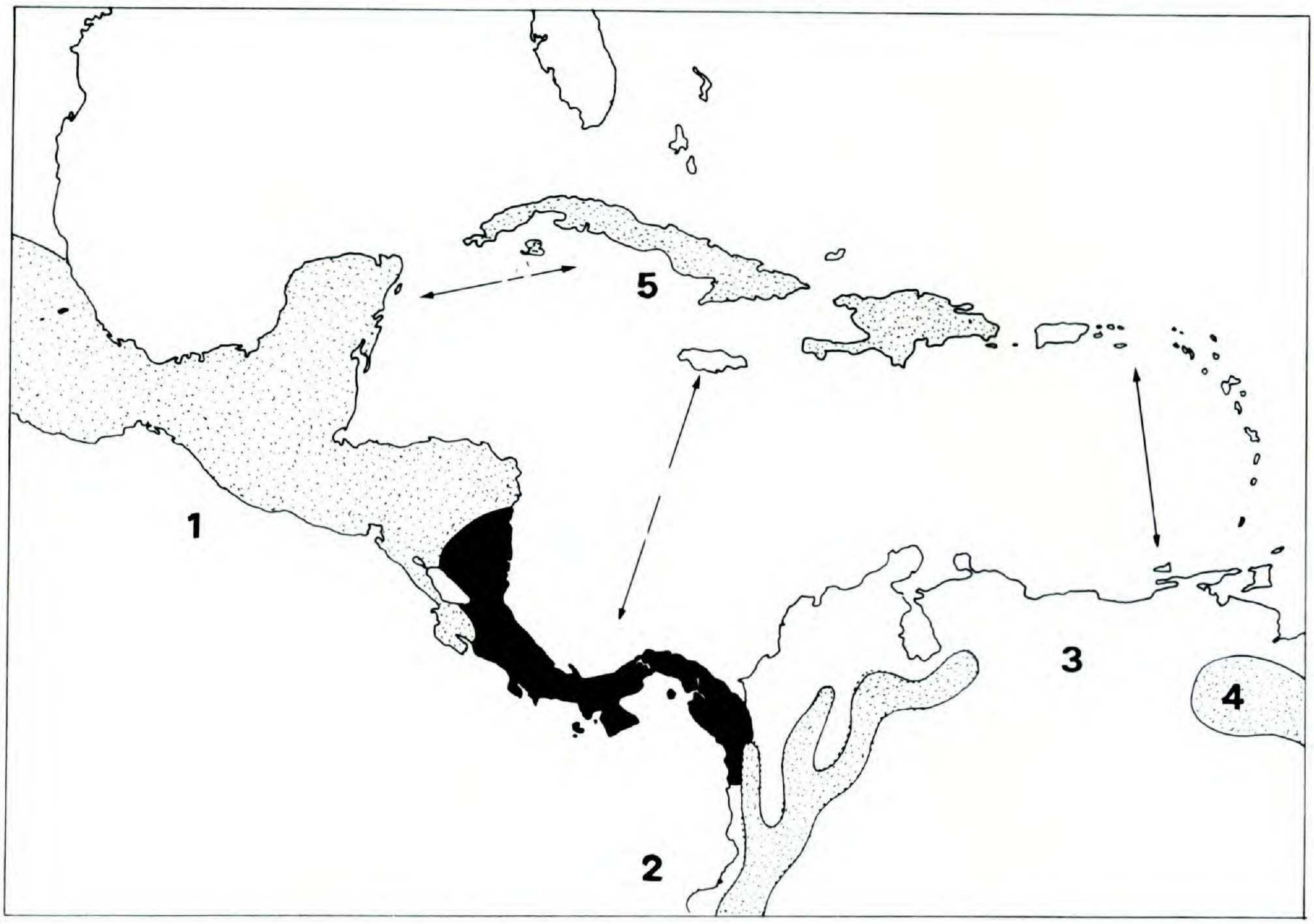

FIGURE 8. The pteridophyte flora of Central America is composed of 1—Mexican-Nuclear Central American elements, 2—Andean, 3—Amazonian, and 5—Antillean. The Guyanan element, 4, is not significant. The solid area indicates higher endemism in the area and the greatest diversity of species per area unit. Arrows indicate areas of greater affinities.

VEGETATION TYPES

Because of its complex geological and climatic history, the Central American Isthmus has been invaded and populated by a series of floristic contingents both from the North and South continental land masses. These vegetations have moved and adopted distributions determined, among many other factors, primarily by edaphic types, rainfall, and altitude. Figure 7 illustrates my concepts of floristic influences, unlike several other vegetation maps, which only detail physiognomic characteristics of the plant cover (Trejos & Archer, 1953; Holdridge, 1957; Lauer, 1960). The proposed eight vegetational elements (Gómez, 1982) are in agreement with the relationships other authors have suggested for various Central American, Mexican and Northern South American localities (Bartlett & Barghoorn, 1973; Beard, 1944, 1953; Breedlove, 1973; Carlson, 1954; Cuatrecasas, 1957; Lundell, 1937; Standley, 1938; Wagner, 1964; Weber, 1958; Werckle, 1909; Williams, 1938). In the eight vegetational zones, the pteridophytes found are those typically associated with or recorded from the parental areas or centers of distribution, with mixed floras occurring along the transitional, bordering lines.

DISJUNCTS

When the flora of a given area is well known, it is easy to spot those organisms that are disjunctive in their distribution. Wagner (1972) has presented and documented the importance of disjunctions in the Pteridophyta of the United States. But neither the Central American floras nor those of immediate neighbouring areas are well known and any interpretation here would run the risk of being potentially misleading. For example, I reported (Gómez, 1973) the presence in Costa Rica of several Mexican ferns, e.g., *Cheiloplecton, Schaffneria,* thought to be endemic to Mexican highlands and subarid areas. The former I have recently collected in Nicaragua and the latter is reported by Stolze (1981) from Guatemala. *Woodwardia* was reported for Costa Rica (Gómez, 1972) as a 1,000-mile disjunct from the nearest Mexican population but it is now known from Guatemala, Honduras, and northern Nicaragua.

There is one spectacular case, that of *Loxsomopsis costaricensis,* an endemic fern with its only other confamiliar in New Zealand. There are no geological indications that Costa Rica and New Zealand were ever connected, not even in the most fertile imagination. Could this case be an indication of a need to review Copeland's (1940) mind-twisting idea of the Antarctic origin of tropical ferns?

The point I am trying to make is that to talk about disjunctions one needs to be certain that there are no intermediate populations of a species between the known and the newly discovered locality.

LONG RANGE DISPERSAL

The preceding lines lead me into a delicate subject I preferred to ignore during the actual presentation of these notes. Professor H. Iltis addressed the one million dollar question by asking What, if not long range dispersal, can explain the distribution of organisms, namely the ferns? I declined to answer then for two reasons: a) the possibility of an ensuing battle between the more or less even numbers of "vicars" vs. "old timers," and b) because the question of long range dispersal would require a symposium of its own and, at that moment, many more minutes at the podium, in itself a horrid prospect . . . .

I do not discard long range dispersal as an effective method of distribution. I do think it is *one* very good way to move about. If I were to reject it, the African bees, Man and other beasts would prove me wrong. But, if that were the only mechanism involved for the air-borne fern spores, I yet have to find clumps of *Matonia, Dipteris, Stromatopteris,* etc., all Old World tropical ferns, growing in my backyard to become a blind adept of this theory. Certainly, the environment itself could never be so selective of those colonizers which readily grow adventitiously around our greenhouses. Even if it were so highly selective there would be problems, such as the one posed by root-parasites and their specific hosts. *Balanophora fungosa* in the Pacific basin and *Prosopanche costaricensis* in Costa Rican rainforests, serve as examples.

Then, what about heterosporous pteridophytes? I find the explanation of *Selaginella peruviana* in southwestern United States and the Peruvian Andes in continental drift and vicariance rather than in long range random dispersal. The many cases of amphipacific, amphiatlantic, and circumboreal disjunctions cannot be explained solely on the basis of continental drift or long range dispersal. In this particular item, what is good for the goose may not be at all good for the gander and scientists have to be careful not to fall prey to excessive fadisms.

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